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The study of animal behaviour has revealed many intricate ways in which individuals deal adaptively with their world, some of which raise controversial issues of interpretation. Scrub jays, for instance, adjust their food-hiding according to the likely competition from other jays. If a competitor has seen them cache food, and they have themselves had the experience of pilfering others' caches, they re-cache in private [1]. If privacy is denied them, they prefer to cache behind barriers, and if there are none they choose ill-lit spots furthest from the competitor [2]. Denied all these options, they fall back on a strategy of confusion, multiply re-caching their foods. These behaviours make good sense, and are easily described in mental-state terms: the jay knows from its own experience how easily a cache can be pilfered by a bird that has seen it made, so tries to keep its competitors ignorant of its own cache sites. In doing so, it takes account of a particular competitor's viewpoint and clarity of vision, and — remembering what a particular competitor is likely to have seen — aims to devalue that knowledge by re-caching somewhere they can't see, or at least confusing the issue by re-caching many times.

In psychology, the ability to model the knowledge and beliefs of others, as distinct from one's own, is called 'theory of mind' [3]. Theory of mind develops slowly in children and may be impaired in autism [4]. Because theory of mind is fundamental to linguistic communication, the attainment has often been thought a crucial step in recent human evolution; but if a bird possesses the same capacity, then our ideas about its evolution will need revising. It is possible, however, to interpret the bird's behaviour quite differently: that it is the consequence of a complex web of associations, each association acquired according to principles well-understood from laboratory study of learning in the white rat. This sort of explanation is sometimes described as conditioning; 'behaviourism' is the philosophy that all learning is fundamentally of this associative nature, even in cases where we experience accompanying mental images and thoughts that seem to suggest otherwise.

To make associative explanations work for such elaborate behaviour patterns, one must take quite a bit on trust. Learning would have to be rapid compared to that of the average laboratory rat, and sharply focused on just those specific features that cure the variables important in explaining how a particular behaviour was learnt. When extended to behaviour of the kind that suggests understanding, in natural environments crowded with distracting features that may all be salient for survival in other ways, associative learning accounts can sometimes appear *unduly* trusting. The attraction, to animal learning theorists, is the chance to de-mystify. Association learning avoids postulating mental states — there is no talk of understanding another's viewpoint, remembering what it saw, and so on — so explanation is grounded in simple phenomena, such as associating two events that often occur together in time and space or repeating behaviour that has previously led to reward. Learning theorists have shown considerable ingenuity in devising associative accounts of apparently impressive, even intellectual, feats of animal behaviour [5,6]. Moreover, the fact that the nervous system undoubtedly does involve synaptic connections of variable

relative strengths forming a complex web of linkages
has encouraged the idea that associative learning is the only right and proper way to understand animal behaviour [7].

Unfortunately, associative accounts can only be tested experimentally in tightly constrained and simplified cases: extension to the complexity of the natural worlds of animals, even that of a jay's food-caching in the laboratory, tends to be a matter of *post hoc* explanation, as in historical sciences, rather than being usefully predictive. Of course, psychologists who study associative learning do experimentally test the predictions made by their theories: but the prediction and testing is local to the confines of highly artificial experimental situations. It is a matter of conviction, not open to verification, when associative learning is extended to account for the many complex and flexible traits observed under natural conditions [8]. The problem can only get worse as explanation moves from the minutiae of single experiments and single adaptive traits to the mentality
of the animal as a whole [9]. The tempting economy or 'parsimony' of postulating only simple theoretical entities needs to be balanced against the power and scope of explanation over the whole range of an animal's abilities: the apparent simplicity of association theory can soon lead to unmanageable complexity in explaining real life.

What is needed is another *level of explanation*, between the massive complexity of the neural networks of the brain, and the simple efficiency of adaptive behaviour in the world. This is where cognitive explanation comes in: *cognition* offers an interlingua between brain and behaviour [10]. Using the conceptual tools of cognitive science — theory of mind, working memory, focus of attention, cognitive map, number concept and counting, procedural knowledge, problem-solving, and many others — allows theories to be developed, simple enough to be comprehended and used to make testable predictions in natural environments, yet tight enough to be mapped precisely onto observed behaviour. (In principle, cognitive explanations can also be meshed with brain structures, but in animal work this is in practice more often a hope for the future, waiting for developments in imaging that can be used under relatively natural conditions.)

An everyday analogy may be made with our understanding of how a television works. There is no doubt that its 'behaviour' — showing moving images of things happening at other places and times — is fundamentally caused by the electronics. However, handing us a full circuit diagram would seldom be educationally helpful. Rather, what is needed is an intervening level of explanation, in which it can be explained that images are sliced up, salami-fashion, then relayed as a linear signal, travelling near-instantaneously along wires as electric waves and across space as radio waves, finally re-assembled by the electronics of the set. Only with the aid of this 'cognitive model' can one start to discuss intelligently the origin of that odd flicker or annoying stripe on the picture, and begin to decide whether it relates to characteristics of the set, the aerial, or the transmitter. The same applies in biology. For an animal as simple as the sea-slug *Aplysia*, with under 20,000 neurons, many of them very large, expecting to explain behaviour directly by tracing neural connections is feasible [11]. But for vertebrates, the combinatorial explosion of possible neural interconnections in the vastly larger brain renders this an impractical task. Indeed, even *Aplysia* has a wider range of behaviour than is understood at the neural level, and a cognitive approach may yet prove useful for this species too.

In behavioural biology, a fundamental goal is to map between brain and behaviour, and the cognitive level of explanation provides an effective tool for doing so. However, cognitive models can be instantiated in material other than flesh and blood: indeed, the origins of modern cognitive neuroscience lie in the development of 'intelligent machines' by Alan Turing and others. Just as a computer program can be run with solid state electronics, or with valves and resistors, or even hydraulic components, so also cognitive models of mental function are semi-independent of hardware. Relying on this freedom, some psychologists have extensively used digital computers to test their cognitive models, as simulations in which the blow-by-blow behaviour of the machine and the human can be compared for match — for example, chessplaying, formal logic and developmental stage-transitions in children's understanding [12,13]. Modern psychology relies almost entirely on cognitive models of behaviour; although few are explicitly tested as simulations, clear and testable predictions can nevertheless be made from these theories, because they are expressed at the 'systems level' of cognition.

The cognitive level of explanation has proved versatile for understanding human behaviour, and in the next few years we can expect see this extended throughout behavioural biology. Already, it is no coincidence that some of the most exciting discoveries in animal behaviour of recent years have begun from a cognitive perspective. As one example, consider the numerical abilities of animals. Chimpanzees, taught the cardinal numbers as Arabic numerals, have proved able to compute simple sums with no explicit training of ordinal number; and knowing numbers extends their abilities [14]. Chimpanzees cannot normally succeed in a task in which the rule is: whichever of two piles of food you point to, your companion gets, and you are left with the other. Trial after trial, a chimpanzee will point to the largest pile, only to be frustrated by the outcome: they simply cannot inhibit their natural attraction to the desired goal. But if Arabic numbers are substituted, they immediately solve the problem and switch to the lower number; if the test reverts to real entities, they again fail.

A grey parrot, Alex, has been taught various human words to facilitate study of its abilities: being a parrot, it is able to speak, but Alex understands appropriate word use rather than merely 'parroting' the words [15]. This has enabled precise testing of Alex's understanding of number. After learning numbers as labels for quantities, he was tested with more complicated arrays of objects: for instance, several blocks and several balls, each coming in two different colours. He was reliably able to answer questions about the size of a specific subset, such as 'How many green balls?', and showed that he understood verbal information of the same sort [16]. This would be an impressive ability for a three-year old child, and it may be that psittacine birds are innately equipped with mathematical concepts that the child only develops slowly during an extended series of interactions with adults.

By questioning whether animals possess or can acquire concepts like ordinal and cardinal number, relative and absolute numerosity, set membership and overlap, these and other fascinating experiments [17] have revealed hidden depths to how animals count the world. No doubt, now that these data are known, learning theorists will manage to devise associative accounts to explain the animals' abilities. The point is not that any particular animal feat will 'disprove' association learning; in fact, associative explanations of realistically complex phenomena are worryingly unfalsifiable. Rather, it is quite unclear how the topic of number and counting could ever have been explored from a standpoint of animal learning theory; and just the same applies to many other current topics in animal behaviour, including social comprehension, spatial knowledge and navigation, imitation and teaching, and everyday understanding of physical systems such as tool use or weather. The advantage of using a cognitive level of description is that it tends to lead to interesting experiments, novel regimes of observation, and theories of naturally adaptive behaviour that can be tested and refined.

Why does any of this need saying, if the advantages of treating animals as cognitive systems are so clear? Where's the controversy? We suspect that the reluctance of biologists to embrace cognitive explanation stems from the elision — in much of the popular and even some scientific writing on animal abilities — between cognition, intelligence and consciousness. The tacit assumption is often made that, if behaviour is best understood as the result of cognitive processes, the animal is showing more intelligence than if an account in terms of association learning will suffice. In fact, ascription of more or less intelligence to animal species is seldom useful, as there is no reliable scale of intellectual differences [18]. Among humans, intelligence measurements are expressed statistically in terms of a reference population's test scores, calibrated against educational achievement. Nothing like that exists for animals, and our everyday judgements of animal 'smartness' are usually based on how well an animal's social system and communicative modality mesh with our own. Worse, the use of cognitive explanation seems to bring a whiff of consciousness along with it.

For those keen to improve animal welfare, this may be manna; while for anyone trained in the dry theorems of animal learning it is anathema, reason enough to strive desperately for an associative counter-explanation. But neither attitude is justified: despite years of fascination with the biological function and brain localization of human consciousness, cognitive theory neither needs nor explains consciousness [19]. Animal consciousness is a fascinating area of debate, but not one likely to be resolved by empirical evidence. Although the root meaning of cognition is thinking, and to many people thinking is a quintessentially conscious activity, from a cognitive perspective thinking is simply a mechanistic, computational process recognizable by its products: thinking enables the thinker to 'go beyond the information given'. The *cognitive revolution* in behavioural and brain sciences was a direct product of the development of computing machines by Alan Turing and others, and the resulting de-mystification of 'mental' processes. Of course, mental states and operations had been discussed for millennia (thought, intention, and reminiscence are not new terms), but from the new cognitive perspective all mental operations were seen as *information processing*. The brain came to be viewed as a device that converts information from one code to another (e.g. from visual to phonological code, when we read silently), stores and retrieves information (from the fleeting traces of immediate visual memory to the laborious recall of events in one's distant past), and operates upon existing information to compute new 'knowledge' (planning future activities and solving problems). A cognitive approach to animal behaviour aims to answer 'how' questions [20], deriving and testing mechanistic theories couched in information processing terms rather than phenomenology, and thus explore the variety of cognitive systems that exist in different species of animal.

Treating animals as cognitive systems is therefore not an approach that should be reserved for the most flexible and human-like species, while the behaviour of simpler animals is safely explained as 'merely' innate or as learned by association (Figure 1). Indeed, whether an animal's behaviour is cognitive, and thus by implication 'clever', or associatively learnt is not an empirical question at all. These are simply two different ways of studying the same behaviour, and in the complex natural environments of most species only the cognitive approach leads to testable predictions.

Why are animals cognitive? One answer is that studying animal behaviour cognitively offers the best chance of understanding the evolution of our own mind — tracing the history of cognition in primate evolution. More generally, the cognitive approach offers the only possibility of dealing scientifically with cases of flexible and sophisticated behavioural abilities in animals, which may prove more widespread in nature than is sometimes obvious from our necessarily anthropocentric viewpoint [21]. This is important, because charting the range of independently evolved, advanced cognitive capacities in many taxa can provide evidence of the biological utility and evolutionary origins of cognition.

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Figure 1. Co-operative hunting has been described in a wide range of animal species: but are similar psychological processes operat- ing in each case?

(A,B) Parties of (usually) male chimpanzees *Pan troglodytes* hunt monkeys, especially colobines, and share the meat extensively with other group members after a kill. Chimpanzee hunting is difficult to observe clearly in their dense, three-dimensional rainforest habitat, but has been claimed to involve rich understanding of the process of co-operation [22], with individuals taking mutually in- terlocking roles, for example 'driver', 'blocker' and 'ambusher', although this remains controversial [23]. (C) Harris' hawks *Parabuteo unicinctus* also hunt cooperatively [24]. Extended families of hawks pursue and kill mammals, particularly rabbits, and it appears to observers that some individuals pursue the prey while others block its escape. (D) Pseudoscorpions are able to kill prey vastly larger than themselves by co-operation [25]; in this illustration, *Paratemnoides nidificator* individuals are attacking the vespid wasp *Apoica pallens* at the Asa Wright Nature Center, Trinidad. Cognitive analyses have not been applied to co-operative hunting in birds or ar- thropods: the assumption seems to be that chimpanzees may 'behave cognitively', whereas other animals can always be explained by simpler processes. This categorization is no more likely to be helpful in biology than those other binary divisions, such as innate *versus* learned, or insightful *versus* automatic, generally seen now as simplistic and misleading. Instead, to make progress it is es- sential to model the competence of each species in the same terms: and these can only be cognitive.